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Altruism during predation in an assassin bug

Alain Dejean · Messika Revel · Frédéric Azémar ·
Olivier Roux

Abstract *Zelus annulosus* is an assassin bug species mostly noted on *Hirtella physophora*, a myrmecophyte specifically associated with the ant *Allomerus decemarticulatus* known to build traps on host tree twigs to ambush insect preys. The *Z. annulosus* females lay egg clutches protected by a sticky substance. To avoid being trapped, the first three instars of nymphs remain grouped in a clutch beneath the leaves on which they hatched, yet from time to time, they climb onto the upper side to group ambush preys. Long-distance prey detection permits these bugs to capture flying or jumping insects that alight on their leaves. Like some other *Zelus* species, the

sticky substance of the sundew setae on their forelegs aids in prey capture. Group ambushing permits early instars to capture insects that they then share or not depending on prey size and the hunger of the successful nymphs. Fourth and fifth instars, with greater needs, rather ambush solitarily on different host tree leaves, but attract siblings to share large preys. Communal feeding permits faster prey consumption, enabling small nymphs to return sooner to the shelter of their leaves. By improving the regularity of feeding for each nymph, it likely regulates nymphal development, synchronizing molting and subsequently limiting cannibalism.

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Introduction

Group hunting followed by food sharing brings fitness benefits to the participants through increased per capita food intake while minimizing the cost of capture. Indeed, in addition to avoiding predation, preys are captured more effectively with less risk of injury. This is known in social spiders (Settepani et al. 2013; Yip and Rayor 2013) and some ant species (Cerdà and Dejean 2011) and, among vertebrates, in fishes (de Waal 2006), birds, cetaceans, otters, carnivorans, and chimpanzees (see the synthesis in Bailey et al. 2013). Harris hawks cooperatively hunt and rear young (Coulson and Coulson 1995). Hyenas, *Lycan*, wolves, and lions also redistribute food between adults (Bailey et al. 2013), as do eusocial insects.

Delayed benefits from food sharing occur in vampire bats which regularly fail to obtain blood, their only food, and die after 70 h if starved. Unsuccessful individuals can receive regurgitations from roost-mates, frequently relatives. Yet, receiving regurgitations depends mostly on having previously provided the helper with blood, resulting in the formation of food-sharing groups characterized by mutual allogrooming

(Carter and Wilkinson 2013). A chimpanzee possessing food, particularly meat, can share it with close relatives or in response to harassment by beggars or obtain a delayed benefit through grooming and forming coalitions according to dominance (Silk et al. 2013). Altruistic motivation for food sharing exists in bonobos which share their food with a stranger rather than with a group mate, but do not give food if a social interaction is impossible (Tan and Hare 2013).

In insects, egg clutching, in addition to improving egg survival by preventing desiccation, is often associated with toxicity or impalatability and favors larval/nymphal aggregation (Janz 2002) which frequently permits early instars to organize a group defense (Jolivet 2008). Feeding efficiency is improved when larval aggregation is associated with communal feeding in the herbivore larvae of sawflies, chrysomelid beetles, and lepidopterans (Wilson 1971; Grégoire 1988). Communal feeding is infrequent among predatory insects that lay their eggs in clutches. Group hunting and prey sharing were noted in the first instar larvae of aphidophagous ladybirds (Moore et al. 2012), in the nymphs and adults of a predacious pentatomid (Heteroptera) (Ables 1975), and in some harpactorine assassin bug nymphs (Heteroptera; Reduviidae) (Inoue 1982; Haridass et al. 1988; Jackson et al. 2010).

Except for the vertebrate blood-feeding Triatominae, other reduviid subfamilies are almost exclusively composed of arthropod predators (Hwang and Weirauch 2012; but see Béranger and Plutot-Sigwalt 1997). Prey capture success in most harpactorine species, related to prey size (Inoue 1985; Cogni et al. 2002), is enhanced by the presence of a sticky substance that coats their legs. “Resin bugs” gather this substance from certain plants (Forero et al. 2011). In some species of the genus *Zelus*, the substance is secreted by specialized dermal glands and sticks to the “sundew setae” (so-called because they resemble the trichomes of sundew carnivorous plants) that cover the tibiae of the forelegs (Werner and Reid 2001; Betz and Kölsch 2004; Weirauch 2006; Zhang and Weirauch 2013). Because they lack these sticky glands, the first instars use the sticky secretions deposited by females on their egg mass to increase their predation success (Weirauch 2006; Law and Sediqi 2010). Also, *Agriosphorus dohrni* nymphs (Harpactorinae) allocate short periods to active foraging where they form search groups of ten or more individuals of different origins (not necessarily siblings); small preys are eaten selfishly, whereas large preys are shared (Inoue 1982, 1985).

The nymphs of the assassin bug *Zelus annulosus* are efficient predators that develop mostly on *Hirtella physophora* (Chrysobalanaceae) (Revel et al. 2010). This is an understorey-dwelling myrmecophyte (i.e., a plant housing ants in hollow structures) whose long-lived leaves bear extrafloral nectaries and a pair of pouches at the base of each lamina where colonies of the myrmicine ant, *Allomerus*

decemarticulatus, shelter. Workers of this species build gallery-shaped traps permitting them to capture preys 1,800 times their weight (Dejean et al. 2005, 2013; Grangier et al. 2008a). *Allomerus* workers tolerate the fragile *Z. annulosus* first instar nymphs on their host plants (these nymphs are thus protected from other ants) and, later, the relatively large last instar nymphs do not attack these ants (Revel et al. 2010). Although several authors have provided information on the predatory behavior of different harpactorine species (Edwards 1966; Inoue 1982, 1985; Haridass et al. 1987, 1988; Weirauch et al. 2012; Zhang and Weirauch 2013), we aimed to verify if clutch laying by females is followed by nymph clustering with the subsequent possibility of group hunting and prey sharing by examining the modalities of their hunting behavior.

Materials and methods

Study site and models

This study was conducted between 2009 and 2013 at the field station at *Petit Saut*, Sinnamary, French Guiana (5°03'39" N; 53°02'36" W) and in the forest around the station; also, some *Z. annulosus* individuals were gathered from *La Montagne des singes* (5°04'19" N; 52°41'42" W), ca. 50 km away from Petit Saut. The climate is tropical moist, with 3,500 mm of annual precipitation distributed over 280 days.

Z. annulosus was only found on pubescent plants, mostly *H. physophora*. The females lay egg clusters under the leaves and deposit a sticky secretion on them that seems sufficient to ward off predators and ants. They then fly away, leaving the eggs to develop unattended. Between 10 and 22 first instar nymphs hatch from these egg clusters (Revel et al. 2010; AD, MR, and OR, personal communication).

The hunting zones and preys of different instars of *Z. annulosus* nymphs

We surveyed 65 *Hirtella* trees on which we had noted the presence of *Z. annulosus* nymphs, representing ca. 240 h of focal samplings distributed over 80 non-consecutive days during the rainy season in which individuals were observed continuously for periods of time of more than 2 h (generally limited by the rain or nightfall). In addition, during a series of observations permitting us to cover the 24 h of the nycthemeron, we verified each hour if the nymphs were hunting or sheltering under the leaves (35 to 43 diurnal controls; 16 to 48 nocturnal controls).

In both approaches, we noted if, depending on the instar, the nymphs stayed under the leaf where they hatched or left to hunt on its upper side, whether they remained grouped or not, and finally if they moved to a different leaf. We also noted what insects were captured by these nymphs plus information

on their size and the period of the year. Using a quartz crystal microbalance, we weighed several live preys and *Z. annulosus* nymphs to calculate the prey–predator weight ratio (Table 1).

Prey capture behavior by *Z. annulosus* nymphs

This study was conducted on nymphs bred in the laboratory in transparent plastic boxes (180×120×75 mm) whose floor was covered with humid blotting paper. Each nymph, starved for 72 h after being placed in the plastic box, was tested only once. The protocol was adapted from that used for solitary foraging ants (see Dejean 2011). During preliminary experiments, a full repertoire of behavioral sequences was first established. Referring to this complete list, the prey capture behavior was studied in the laboratory using third ($N=56$) and fifth ($N=28$) instar *Z. annulosus* nymphs confronted with termite workers (*Nasutitermes nigriceps*) which are easy to find and rather uniform in size. After a prey was dropped from ca. 50 mm in height, we recorded the complete sequence of behavioral acts performed by the nymphs until they abandoned the remains of the prey. We then built flow diagrams where the transition

Table 1 Information on the predator–prey weight ratio for the different cases studied. The weight of the *Zelus annulosus* nymphs and adults corresponds to an average for five to ten individuals starved for 4 days

	Size (mm)	Weight (mg)
<i>Z. annulosus</i>		
First instar nymphs	4	2.8
Second instar nymphs	5–6	6.0
Third instar nymphs	8–10	17.0
Fourth instar nymphs	12–14	35.5
Fifth instar nymphs	18–20	63.0
Adults	21–24	67.5
Ratio between the weight of experimental prey and <i>Z. annulosus</i> nymphs		
<i>Nasutitermes nigriceps</i> workers		
First instar nymphs	4–5 mm	9–12 mg
Second instar nymphs	3.21 to 4.28	
Third instar nymphs	1.50 to 2.00	
Fourth instar nymphs	0.53 to 0.71	
Fifth instar nymphs	0.14 to 0.19	
Tipulidae		
Third instar nymphs	27–30 mm	17–25 mg
Third instar nymphs	1 to 1.47	
Grasshoppers		
Third instar nymphs	10–12 mm	35–44 mg
Third instar nymphs	2.06 to 2.59	
Katydids		
Second instar nymphs	12–14 mm	80–100 mg
Second instar nymphs	13.33 to 16.67	
Fourth instar nymphs	2.53 to 2.82	
Fifth instar nymphs	1.27 to 1.59	
Katydids		
Second instar nymphs	19–20 mm	135–150 mg
Second instar nymphs	22.50 to 25.00	
Third instar nymphs	7.94 to 8.82	

frequencies between behavioral acts, presented as percentages, were calculated based on the overall number of cases.

Role of the sundew setae during the capture of flying and jumping insects

We tested third instar nymphs bred in the same laboratory conditions as previously but using larger transparent plastic boxes (240×180×100 mm) inside which we installed a paper shelf in one corner of the box, 20 mm below the cover. Two sets of 14 nymphs were starved for 72 h before one set was provided with 27–30-mm-long adult Tipulidae and the other with 10–12-mm-long grasshoppers. Each nymph was tested only once. The tested preys were first placed in a refrigerator at 4 °C during 30 min before being very gently deposited on the paper shelf in the plastic boxes so as to keep them from being immediately detected. They remained immobile during 5–6 min before leaving the paper shelf and were captured when they happened to walk close to the ambushing nymphs. We noted the behavioral sequences.

Prey sharing by *Z. annulosus* nymphs: influence of prey size, predator size, and degree of hunger

We verified if first instar nymphs, although fragile in appearance, are able to capture and share preys. Using smooth forceps, we gathered nine groups of nymphs and placed each group in a transparent plastic box and transported them to the laboratory. After starving them for 24 h and still using smooth forceps, we deposited them on the upper side of a horizontal *H. physophora* leaf placed in the plastic boxes. After 5 min, the nymphs apparently adapted to this situation as they did not immediately move under the leaves and remained grouped. We dropped a termite from ca. 50 mm in height onto the center of the leaf and noted if the nymphs captured and shared the prey.

We tested the influence of the degree of starvation and the size of the preys in a series of experiments based on groups of five or six second instar nymphs. We bred them in transparent plastic boxes (240×180×100 mm) where we placed an old, resistant *Hirtella* leaf (they have an acumen; see Grangier et al. 2008a) maintained 30 mm above the floor, thanks to a piece of modeling clay. Also, a small test tube containing cotton imbibed with water served as a watering place. After being starved for 96 h, 14 groups of nymphs were provided with one termite worker; we verified if the nymphs shared the prey. After the same period of starvation, 14 other groups of nymphs were provided with 12–14-mm-long katydids and here, too, we verified if the preys were shared; 36 h later, we provided these 14 groups (they were not yet food deprived as they had eaten a katydid 36 h before) with a termite worker and again noted if the preys were shared or not.

Further observations were made in the forest to verify if the behaviors differed from those noted in the laboratory. We also

tested if second instar nymphs gathered from plants originating from different geographic areas (i.e., Petit Saut and La Montagne des singes) tolerate each other by creating eight mixed groups (three individuals from each site) that were bred in transparent plastic boxes (180×120×75 mm) whose floor was covered with humid blotting paper. We furnished them with 19–20-mm-long katydids as prey and verified if the nymphs remained grouped, if there were signs of aggressiveness, and if they shared these preys.

Are nymphs attracted when preys are shared by late instar *Z. annulosus* nymphs?

Late instar nymphs fan out over different *Hirtella* leaves to ambush (MR, personal communication). Because we noted that they shared preys, we hypothesized that a successful nymph can attract tree-mates. Due to the horizontal position of *Hirtella* leaves, it was easy to eliminate the visual cues that can attract individuals ambushing on lower leaves by placing a prey on one of the upper leaves. We very gently placed a 12–14-mm-long numbered (by freezing) katydid on the uppermost leaf of each surveyed *Hirtella* tree while fourth or fifth instar nymphs were ambushing on lower leaves and noted the number of nymphs present on that leaf after 30 min of feeding on the katydid. We compared two situations (25 cases each): absence (control) versus presence (trial) of an ambushing nymph on the upper leaf when we deposited the katydid.

In 22 cases similar to the previous control (here control 1), we noted the length of time separating the depositing of the katydid from the arrival of a first nymph. For 11 of these cases, we waited until a second nymph arrived (trial 1); for the 11 other cases, we removed the first nymph prior to it attacking the katydid (control 2). In both cases, we noted the length of time separating the arrival of the first and second nymphs. These data were compared with 15 cases where a nymph was ambushing on the upper leaf, noting the length of time separating the depositing of the katydid from the arrival of a “second” nymph (trial 2).

In a third experiment, conducted on 16 *Hirtella* trees sheltering last instar *Zelus* nymphs, we deposited two katydids on two lower leaves while a nymph was ambushing on one of them. We compared the length of time separating the depositing of the katydids from the arrival of a nymph on each of the two leaves. Statistical analyses were conducted using GraphPad Prism 5.02 software.

Results

The hunting zones and preys of different instars of *Z. annulosus* nymphs

In the field, the first instar nymphs remained grouped under the leaf where they hatched until the first molt and only

exceptionally climbed up onto the upper side of that leaf where they all sat and waited, their forelegs upward, ambushing in a group (noted once for eight groups monitored hourly between 8:00 and 18:00 hours during six non-consecutive days). The second and third instar nymphs devoted much more time to group ambushing on the upper side of their leaves (noted 28 times for the eight groups monitored during 12 non-consecutive days, the two instars pooled; comparison with the previous case, Fisher’s exact test: $P < 0.001$). The rest of the day and at night, nymphs of all stages remain grouped under the protection of their leaves; hunting nymphs immediately sheltered under the leaves when the rain began (27 cases noted). We observed that less than 5 min separated the moment when the first and the last individual climbed up onto the upper side of their leaf to ambush in a group. On the contrary, diurnally, the fourth and fifth instar nymphs mostly ambushed solitarily on different leaves as they are large enough to avoid the traps built by *Allomerus* ants as they slowly move from leaf to leaf. This was the case for 47 observations out of 96 (12 series of observations of eight groups, the two instars pooled; 48.9 %), but twice they were grouped on a leaf (2.1 %; but see below).

Because they ambush on the leaves of their host trees, *Z. annulosus* nymphs captured flying insects almost uniquely, the exceptions being jumping Orthoptera nymphs (Table 2). The second instar nymphs captured only small (i.e., less than 8 mm), fragile preys (i.e., Aleyrodidae and different Diptera; likely underrepresented in Table 2), while larger instars attacked almost all insects that tried to land on their leaf, including items larger than themselves. Seasonality was noted for certain preys as all horse flies were captured in October (when they abound during the dry season), winged termites were captured after the first rains in December and January and winged ants between mid-December and March.

The *Z. annulosus* nymphs can feed on the prey captured by the *Allomerus* on their trap (cleptobiosis was noted nine times) or on flies, social wasps, and stingless bees attracted by these captured preys.

Prey capture behavior by *Z. annulosus* nymphs (laboratory studies)

The predatory sequences developed by small and large *Z. annulosus* nymphs were quite similar although the predator–prey weight ratios were different (see Table 1). When ambushing, nymphs generally lift and spread their forelegs. Preys, detected from a distance by visual or chemical cues or vibrations, were cautiously approached; the nymphs lifting their forelegs higher than previously. When at an adequate distance, they slammed their forelegs down on the preys stuck on the sundew setae; then, the nymphs extended their rostrum toward the preys to bite them in an inter-segmental zone, paralyzing them. The *Z. annulosus* lifted the preys by

Table 2 Different arthropod taxa captured under natural conditions by *Zelus annulosus* ($N=308$)

Insect prey	Size (mm)	No. of cases	Insect prey	Size (mm)	No. of cases
Ephemeroptera (mayflies)	24	1	Thysanoptera, Thripidae	6–7	11
Odonata, Lestidae (damselflies)	23	1	Neuroptera, Chrysopidae	12–14	2
Orthoptera	–	–	Coleoptera	–	–
Tettigoniidae (katydids)	11–15	15	Chrysomelidae	6–15	23
–	>25	6	Lampyridae (fire flies)	11–13	3
Gryllidae (crickets)	11–15	8	Cerambycidae	21	1
–	>25	2	Diptera	–	–
Acrididae (grasshoppers)	11–15	12	Culicidae and Cecidomyiidae	7	6
–	>25	4	Tachinidae and Calliphoridae	<10	24
Mantodea (praying mantises)	24	1	(Flies)	>10	4
Blattaria (cockroaches)	–	–	Tabanidae (horse flies)	11	14
–	<25	17	Tipulidae (crane flies)	15–18	17
–	25–40	8	–	30–35	11
Isoptera (termites)	–	–	Drosophilidae (fruit flies)	<5	20
Winged termites	10–15	12	Other flies	4–6	13
Dermaptera (earwings)	14	1	Lepidoptera	–	–
Psocoptera	5	2	Rhopalocera (butterflies)	20–22	7
Hemiptera	–	–	Heterocera (moths)	11–25	6
Aleyrodidae	6–7	4	Hymenoptera	–	–
Cicadellidae	7–8	2	Ichneumonidae	24–28	2
Membracidae	8–10	2	Vespidae, Polistinae	–	–
Fulgoromorpha	8–12	2	<i>Angiopolybia pallens</i> ^a	11	7
Sap-sucking Heteroptera	12–18	7	Formicidae (winged)	7–16	17
Reduviidae (assassin bugs) ^a	20–22	4	Apidae; <i>Trigona</i> ^a	11	9

^a Attracted by a prey already in the process of being eaten by *Zelus annulosus* nymphs and captured in turn

extending their rostrum and later used their forelegs to rotate the preys while injecting saliva and sucking out digested matter; the corresponding parts of the preys turned black. The *Z. annulosus* nymphs can repeatedly rotate and bite the preys up to ten times before discarding the emptied out preys (Figs. 1 and 2).

Role of the sundew setae during the capture of flying and jumping insects (laboratory studies)

Both tested preys were detected by sight immediately after they began to leave the paper shelf on which they had been deposited; indeed, the nymphs oriented their bodies in the preys' direction while lifting their antennae and forelegs. The attacks occurred immediately after the preys happened to approach the nymphs to less than 20 mm. All of the 14 tested Tipulidae were captured in flight on the first attempt as one or both of their long, thin wings became stuck to the nymphs' forelegs and they became paralyzed after being bitten. Among the 14 tested grasshoppers, 10 (71.4 %) were mastered on the first attempt because they lost their hind legs through autotomy at contact with the sundew setae of the *Zelus* nymphs' forelegs (see Fig. 2d). Among the four

remaining grasshoppers, three were mastered on the first attempt although they did not lose their hind legs and the last one escaped. Here, too, the bite triggered immediate paralysis. As was noted for termites, after becoming paralyzed, both the Tipulidae and the katydids were rotated and bitten numerous times before being abandoned.

Prey sharing by *Z. annulosus* nymphs: influence of prey size, predator size, and degree of hunger (laboratory studies)

All tested groups of starved first instar nymphs almost simultaneously attacked and then shared a termite prey.

Although the size between termite workers and katydids is not the only difference, the importance of prey size likely explains the difference noted when starved groups of second instar nymphs shared a termite worker in only 28.6 % of the cases, while they shared a much larger katydid in all cases. The effect of hunger was illustrated as 36 h after capturing a katydid as prey these “rather replete” nymphs this time shared a termite worker in 92.8 % of the cases (Fig. 3; see also prey sharing in natural conditions in Fig. 2).

When the captured termites were not shared, the nymph that successfully captured them moved away from its siblings.

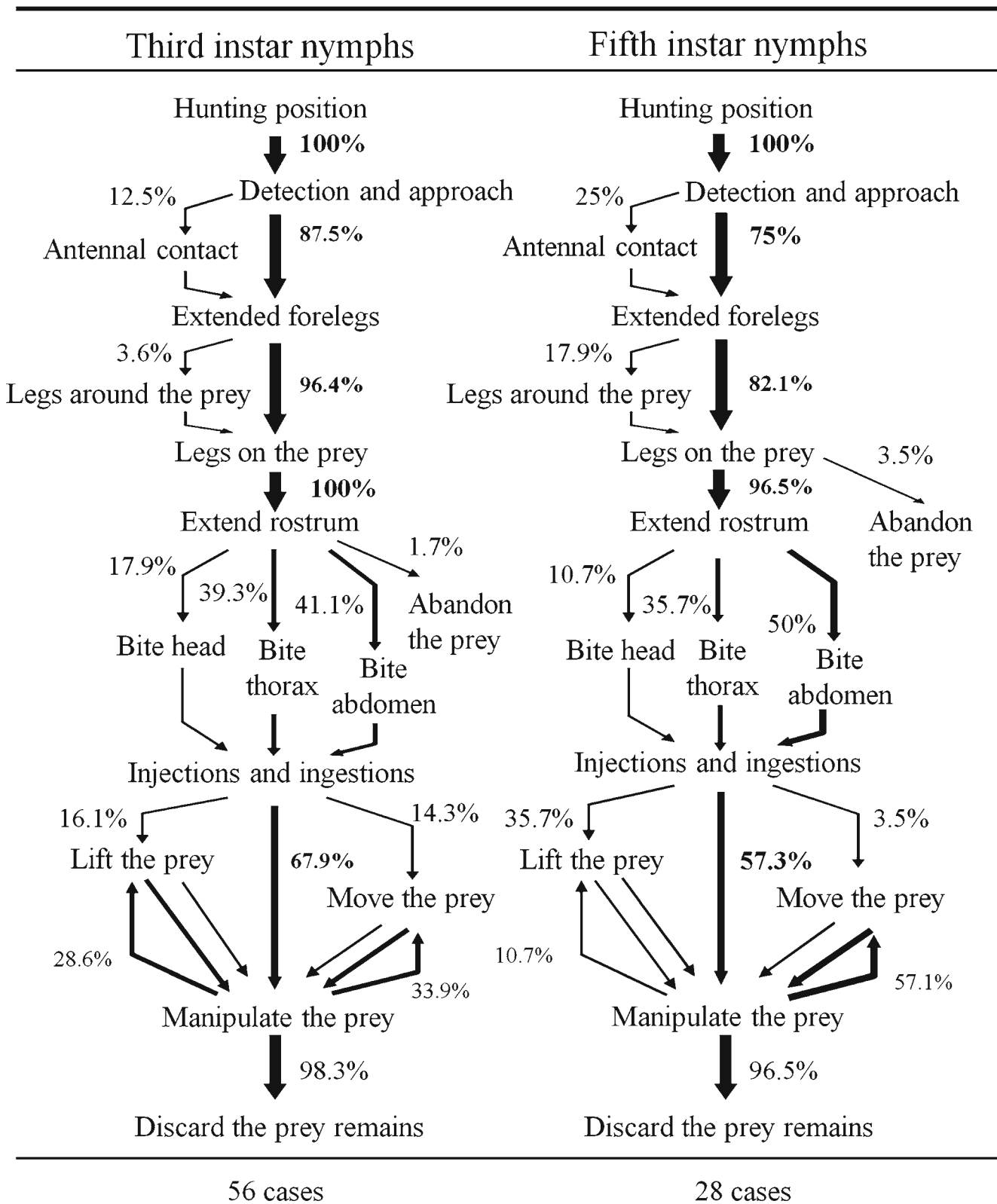
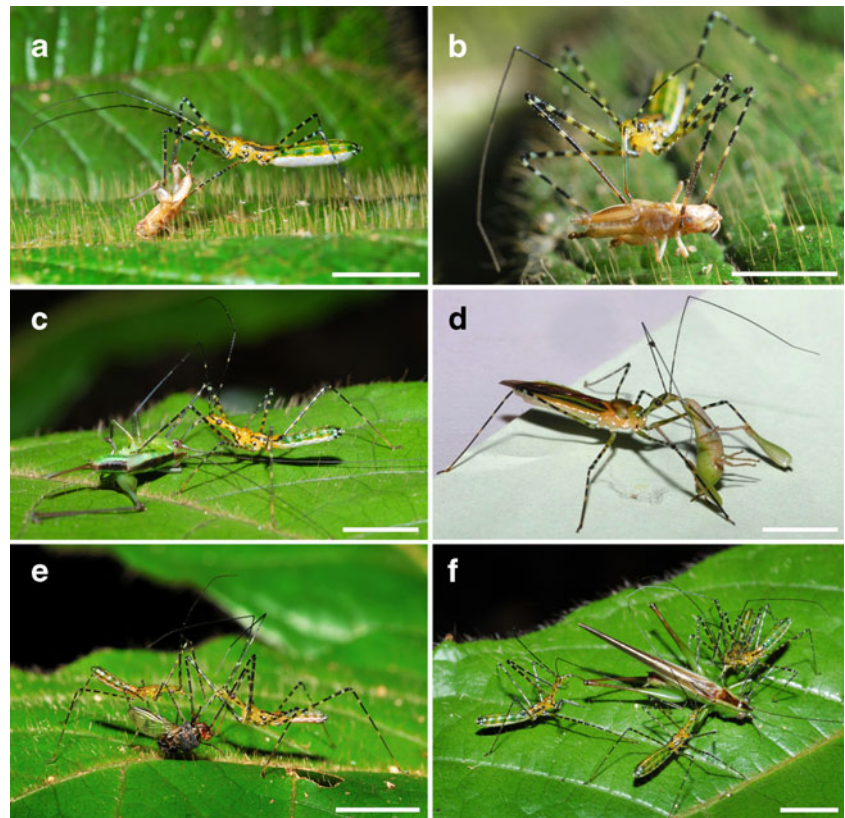


Fig. 1 Flow diagrams representing the sequences of the hunting behavior of *Z. annulosus* nymphs of two size classes during the capture of termite workers. The percentages were calculated from the total number of cases

Fig. 2 Capture of grasshoppers and katydids by *Z. annulosus*. **a** A small grasshopper was just seized and bitten by a fifth instar nymph. **b** A grasshopper is rotated and bitten in several parts. **c** A katydid nymph was just captured by a fifth instar nymph and had lost one hind leg in the process. **d** A small grasshopper, captured by an adult *Zelus*, had lost its hind legs through autotomy; the latter are still glued to the forelegs of the *Zelus*. The horizontal bars represent 10 mm. **e** Two nymphs sharing a fly. **f** An adult katydid was captured by a fifth instar nymph and is now being shared with three other nymphs, one of them biting this prey on the joint between the femur and the tibia of the hind leg



At the end of the sequence, it walked to the tip of the *Hirtella* leaf, placed its head above the extremity of the narrow acumen, and selfishly ate the termite. Indeed, none of the other nymphs tried to reach the prey from the underside of the leaf, and it was out of their reach from the upper side. The same was noted for five cases during controls conducted in the forest.

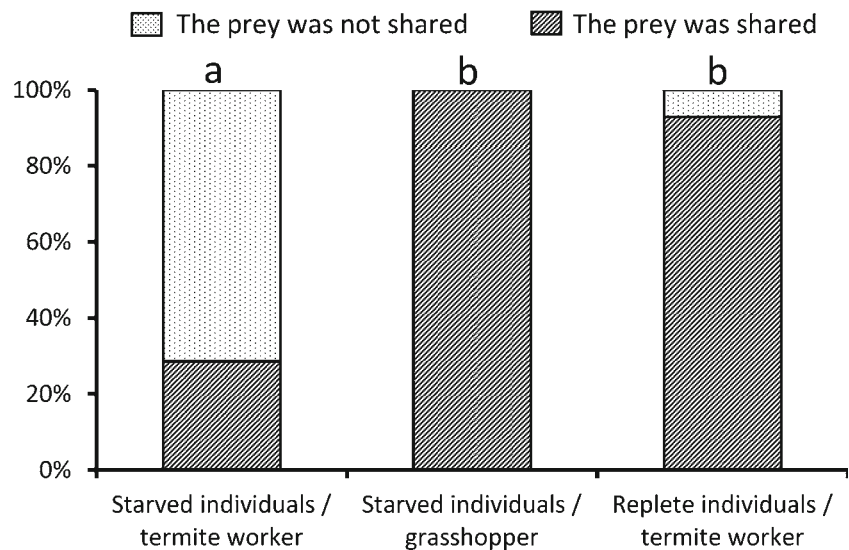
When testing if *Z. annulosus* nymphs from different geographic areas can form mixed groups, we noted that nymphs

from all eight artificial groups remained grouped exactly as did siblings and that they similarly shared the tested preys.

Are nymphs attracted when preys are shared by late instar *Z. annulosus* nymphs?

From field studies, we have gathered arguments showing that *Z. annulosus* nymphs successful at capturing a prey likely

Fig. 3 Prey sharing according to its size and the degree of hunger of second instar *Z. annulosus* nymphs ($N=14$ in each case). Statistical comparison: Fisher's exact tests; simultaneous tests were adjusted using the false discovery rate ("BY" correction as the P values are not independent; Pike 2011); different letters indicate significant differences at $P<0.01$



attract siblings; the tests being based on comparing nymphs attracted toward a prey alone (controls) to their attraction to a prey already having been captured by a sibling (trials). First, 30 min after a nymph had begun to feed on the numbed katydid provided, we noted significantly more nymphs on these leaves (trial) than on control leaves (2.64 ± 0.21 vs. 0.36 ± 0.11 ; $N=25$ in each case; Welch's corrected t test: $t=9.371$; $df=36$; $P<0.0001$). Second, we did not note a significant difference between control 1 (length of time separating our depositing a numbed katydid and the arrival of a first nymph) and control 2 (when we removed the first nymph that reached the leaf where we had deposited the katydid) (Fig. 4). The length of time corresponding to these controls was significantly longer than that corresponding to trial 1 (i.e., separating the arrival of the two first nymphs) and trial 2 (i.e., an ambushing nymph was already present), while the difference between these latter situations was not significant (Fig. 4). Third, the length of time separating the depositing of katydids onto two lower leaves of 16 *Hirtella* trees to the arrival of a "new" last instar nymph was significantly shorter when a *Zelus* nymph was present (trials) than for the controls (25.5 ± 1.9 vs. 14.3 ± 0.9 min; paired t test: $t=5.47$; $df=15$; $P<0.0001$).

Discussion

Although they are apparently fragile and never leave the underside of the *H. physophora* leaves where they hatched (Revel et al. 2010) since they risk being trapped by *Allomerus*

ants, we show that *Z. annulosus* first instar nymphs are able to capture and share comparatively large preys of up to 4.28 times their weight (Table 1). This capacity likely permits them to avoid lethal starvation which is recurrent in tropical species (Maran and Ambrose 2000). In natural conditions, few flying insects of adequate size are prone to alight under the leaves of their host plant so that their main preys are adults of gall-making Cecidomyiidae, which are frequent under the leaves of shrubs in the understorey (AD, personal observation).

The sequences of behavioral acts during prey capture by solitary nymphs were very similar to those known for other Harpactorinae, except that *Z. annulosus* ambush preys and detect them from a "long" distance, while, in other species, the nymphs forage actively and frequently detect the preys through antennal contact (Edwards 1966; Inoue 1982, 1985; Haridass et al. 1987, 1988; Jackson et al. 2010; Weirauch et al. 2012). Sundew setae are known to play an important role in the capture of caterpillars and small flying insects (Weirauch et al. 2012; Zhang and Weirauch 2013). Here, we show that they permit the capture of large insects prone to escape easily by flying or jumping away. Furthermore, contact with the sundew setae of the *Zelus* nymphs' forelegs triggered the autotomy of the hind legs of a grasshopper in 10 out of 14 cases. Autotomy, a mechanism designed to help an insect elude a predator's grasp, occurred here at the expense of the prey. Finally, in all cases, the injection of saliva was determinant due to its fast, non-lethal paralytic effect related to the presence of neurotoxic compounds (see Maran and Ambrose 2000; Corzo et al. 2001; Sahayaraj and Vinothkanna 2011).

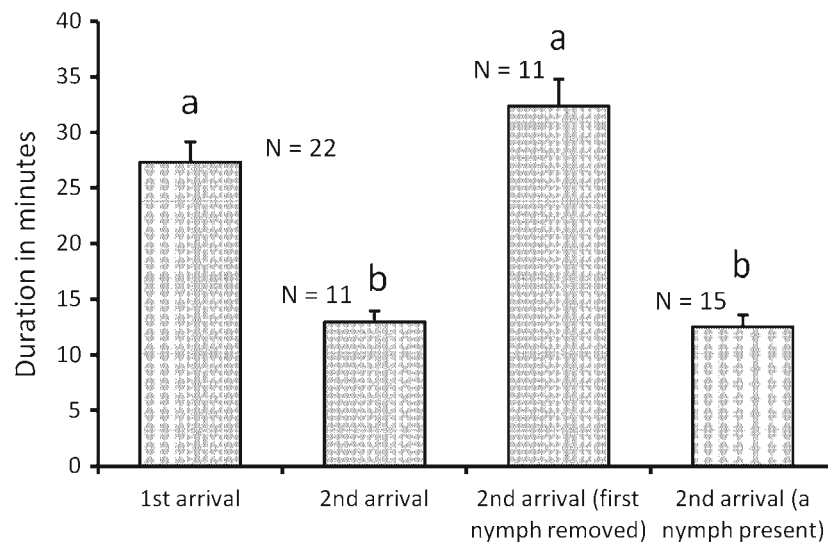


Fig. 4 Comparison of the length of time (means \pm SE) between (1) our depositing of a numbed katydid on the uppermost horizontal leaf of *Hirtella* trees and the arrival of the first *Z. annulosus* nymph (control 1 in the text), (2) the arrival of the second nymph (experiment 1), (3) the arrival of the second nymph, whereas we had removed the first nymph that reached the leaf where we had deposited the katydid (control 2), and

(4) between our depositing of a numbed katydid on the uppermost horizontal leaf on which a nymph was already ambushing and the arrival of a second nymph (experiment 2). Statistical comparison; ANOVA: $F=19.77$; $P<0.001$; Newman-Keuls post hoc test: different letters indicate a significant difference at $P<0.001$

Communal nymphal feeding on large preys has been reported in several harpactorine species (Inoue 1982; Haridass et al. 1988; Jackson et al. 2010). Although *A. dohrni* nymphs are active foragers while *Z. annulosus* nymphs are ambushers, in both species, small preys are eaten selfishly, whereas large preys are shared (Inoue 1982, 1985; this study). The groups of *Z. annulosus* nymphs are formed of siblings originating from the same egg clutches that ambush together and almost simultaneously attack large insects. So, peaceful food sharing may be related to kin selection (Hamilton 1964). Yet, although they generally form groups of siblings in nature, we show that *Z. annulosus* nymphs tolerate non-kin conspecifics and even share preys with them as did *A. dohrni* nymphs in nature (Inoue 1982). Note that the tolerance of conspecific aliens exists in the very similar situation of *Allomerus* plant-ants associated with *H. physophora* or *Cordia nodosa*, another myrmecophyte (Grangier et al. 2008b; see also papers cited therein).

It is probable that group living enhances protection from predators in early instar *Z. annulosus* nymphs as flying insects, mostly social wasps, regularly visit their host trees, trying to steal preys from the *Allomerus* ants (Dejean et al. 2012). This predation pressure explains why these nymphs stay underneath the leaves where they hatch. Because *Z. annulosus* nymphs remain immobile, insect predators may have trouble locating them when they are in the shade of their leaves and, because they remain grouped, they successfully counter-attack enemies. Communal feeding, which occurs for comparatively large insects (see prey–predator weight ratios in Table 2) plus small preys when the nymphs are replete, likely permits the effective exploitation of resources by pooling saliva and enabling a more rapid external digestion (see Schaefer 2003; Forthman and Weirauch 2012). The passage from selfishness to altruism through the “passive” sharing of small preys according to the degree of hunger of the nymphs, whereas large preys are shared, could regulate the food intake between nymphs, facilitating their synchronous development and molting. This limits size differences between the individuals of each group, a factor favoring cannibalism in assassin bugs, particularly for molting nymphs (Inoue 1983).

The main novelty of this study is the presence of “active” sharing for late instar nymphs that attract siblings to feed communally on large preys although they hunt solitarily on different leaves, but we do not know if this attraction is due to pheromones or vibrations, both being known in Hemiptera (Kölliker et al. 2006; Nomakuchi et al. 2012; Kavčič et al. 2013). The fact that these nymphs ambush on different leaves and can attract siblings to share large preys increases the probability that each of them feeds regularly, while here, too, favoring the synchronization of the development and molting of the nymphs (see the similar size of the nymphs in Fig. 2f), limiting cannibalism. Because the preys are very attractive to predatory social wasps and stingless bees (Dejean et al. 2012), the faster the siblings arrive, the less chance there is that a

successful nymph will have its prey stolen or even be killed in turn. Moreover, arriving siblings can capture these cleptobionts (see Table 2) as do *Allomerus* ants (Dejean et al. 2012). Sharing large preys can result in a “by-product benefit” for the others (i.e., no cost for the donor, a benefit for the receiver; Leimar and Connor 2003) or a “food for food” mutualism when a previous donor can later share a large prey captured by one of its siblings (see Stevens and Gilby 2004).

As a result, it is likely that communal feeding by *Z. annulosus* nymphs permits siblings to reduce the likelihood of starvation, decrease the time of exposure to predators, synchronize the development of siblings limiting the possibility of cannibalism while permitting the continuity of equitable mutual prey sharing, and finally increase their probability of reaching adulthood. The whole occurs through a self-sustaining process regulated by simple rules such as clutch laying triggering group living and ambushing by early instars (non-kins are tolerated), sharing a prey or not depending on its size and the degree of hunger of the successful nymph, and last instars attracting siblings to share large preys.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards The experiments comply with the current laws of the country in which they were conducted.

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